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Embryogeny of *Sarcandra glabra* (Thunb.) Nakai (Chloranthaceae) and Phylogenetic Position of the Chloranthaceae

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The development of embryo of *Sarcandra glabra* was described. The formation of embryo had the T-shaped proembryo at the beginning and the initial cells of the root-cortex were derived from the lowr tier of the cell *m*, so the embryonic development was conformed to the Polygonad type. It seems that the Chloranthaceae has closer affinity to the Polygonales and the Caryophyllales than the Magnoliales.

Engler and Plantl (1894) treated Piperales (including Chloranthales) as one of the most primitive order in the Dicotyledons. Rendle (1937) considered that the Piperales (including Chloranthaceae) were allied to the Polygonales. Recently, many authors considered that the Piperales and the Chloranthales were derived from Magnoliales (Swamy 1953, Takhtajian 1954, Melchior 1964, Carlquist 1964, Cronquist 1981 and Endress 1987). Many of them have considered that, within the Magnoliidae, the floral morphology of Lactridaceae or Trimeniaceae showed some similar construction with the Piperales and the Chloranthales. They were regarded as a group with reduced forms of the Magnoliales.

The flower of the Lactridaceae consists of three perianths, six stamens in two rows and three carpels. These floral elements were arranged with the alternate order and were fundamentally arranged in the reduced form of the Magnoliaceous flower (Carlquist 1964). In the Trimeniaceae stamens are spirally inserted on receptacle independent of perianths. On the other hand, the Piperales and the Chrolanthales have various floral construction. Nevertheless the flowers have the fundamentally common feature with bracts (the so-called perianths in *Hedyosmum*, Yamazaki 1992), stamens and carpels are arranged in opposite order as in those of Amentiferae. Therefore, the Piperales and the Chrolanthales have less phylogenetic affinity with the Lactoridaceae or the Trimeniaceae.

From the study of *rbcL* DNA sequences, Chase et al. (1993) treated with Piperales and the Chrolanthales in the Paleoherbs which were those of the primitive Angiosperms.

Method of embryonic development reveal an important data in the study of the Angiosperms (Yamazaki 1982). Embryonic development in the Chloranthacea was studied in *Chloranthus serratus* Roem. et Schult. (Yoshida 1959a) and *Sarcandra irvingbaileyi* Swamy (Vijayaraghavan 1964), but these reports were insufficient to discuss the phylogenetic affinity based on embryonic development. The present work of embryonic development on *Sarcandra glabra* is an attempt to contribute to the phylogenetic relationships in the Chloranthales.

Materials and Methods

Flowers and fruits were collected from cultivated plants in Botanical Gardens, Faculty of Science, University of Tokyo, in July to October, 1994 to 1997. The materials were fixed in an alcohol-formalin-acetic acid, and imbedded in paraffin in the usual way. Serial sections, 12–14 μm thick, were cut, and stained by Heidenhain's hematoxylin and fast green.

Results

Ovule and embryo sac. Ovule is orthotro-pous, bitegmic, and crassinucellar, with the micropyle formed by both integuments (Fig. 1-1). The megaspore mother cells lie in a linear tetrad, and the chalazal one develops into an embryo sac. These embryosac formations have been reported by Yoshida (1959b), and will not be described in the present paper.

Embryogenesis. The first division of the fertilized egg is transverse resulting in the formation of the terminal cell *ca* and the basal cell *cb* (Fig. 2: 1). The cell *ca* divides vertically, while *cb* undergoes a transverse division producing cells *m* and *ci*. The four-celled proembryo is in T-shaped (Figs. 2: 2, 3). The terminal cells *ca* divide vertically to form four cells. Each of four cells undergoes repeatedly transverse and vertical divisions to form the vegetative apex, two cotyledons and the upper part of hypocotyl (Figs. 2: 6–12). In earlier stages the cell *m* undergoes vertical divisions repeatedly (Figs. 2: 4–12) and in many celled proembryo stages each of these cells undergoes transverse divisions to form two tiers (Fig. 2: 13). The upper titer of *m* repeatedly divides transversely and vertically to form the lower part of hypocotyl. The lower tier of *m* produces the initial of root-cortex (iec) in the center (Figs. 2: 14, 15). The lower cell *ci* divides transversely to form *n* and *s* (Figs. 1: 2, 2: 4). The cell *n* slowly divides transversely and vertically to form the root cap (Figs. 2: 14, 15). The cell *ci* divides to form the suspensor (Figs. 2: 13, 14).

The recapitulatory table is as follows:

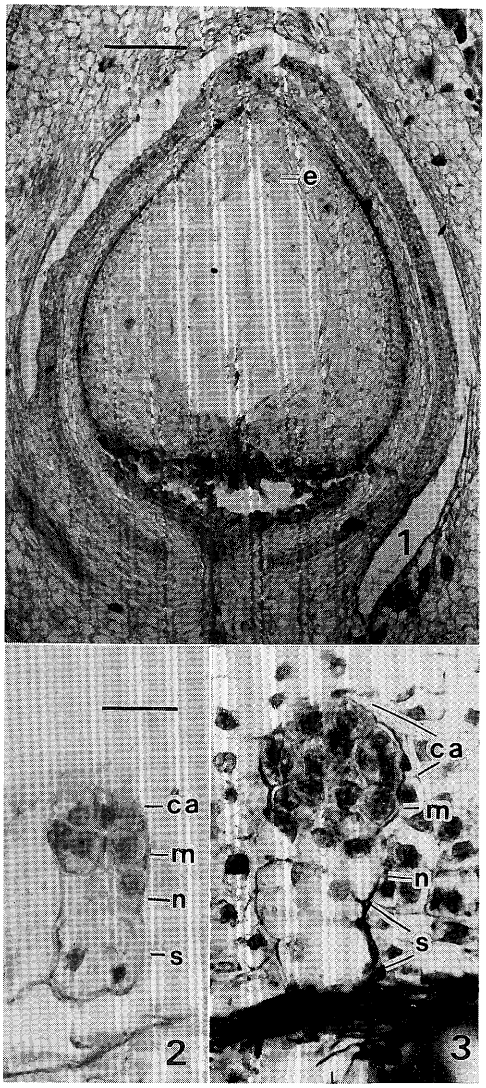
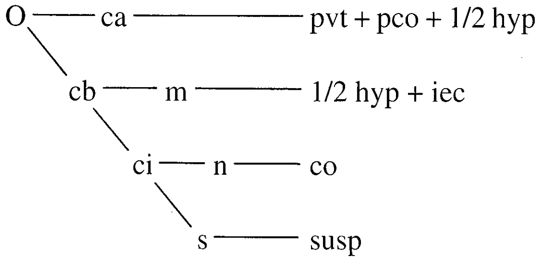


Fig. 1. 1, transverse section of ovule. e, fertilied egg. 2 and 3, young stages of embryo. Abbreviations in text. Bar 1 = 0.2 mm. 2 and 3 = 50 μm.



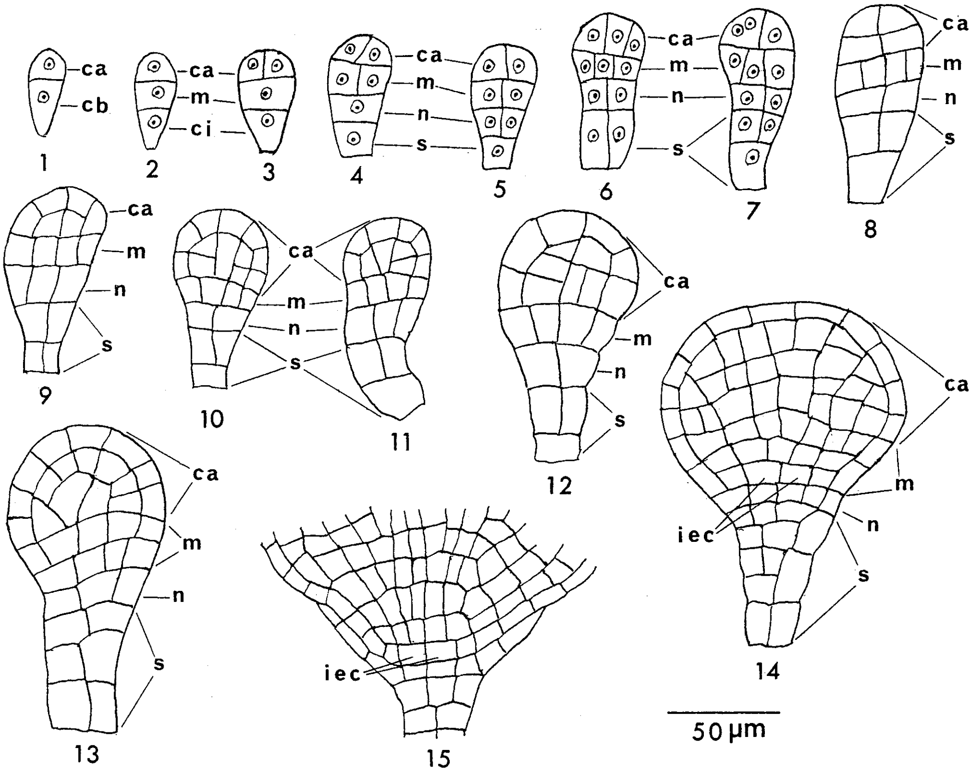


Fig. 2. Stages of development of embryo. Abbreviations in text.

Abbreviations. pvt, provegetative apex. pco, procotyledon. phy, prohypocotyl. iec, initial cells of root-cortex. co, root-cap. susp, suspensor.

Discussion

The development of embryo of *Sarcandra glabra* is fundamentally the same as that of *S. irvingbailleyi* reported by Vijaraghavan (1964). He determined that the embryonic development of *S. irvingbailleyi* confirmed to the Onagrad type by the T-shaped pro-embryo. However, in the Onagrad type the initial cells of root-cortex directly derives from one cell originated from the upper part of tier *m*. In *Sarcandra* spp. the initial cells of root-cortex were derived from a few cells originated from the lower part of the tier *m*, and the embryonic development of *Sarcandra* spp. is conformed with the Polygonad type as previously described by the author (Yamazaki 1982). The embryonic development of *Houttuynia cordata* Thunb. in Saururaceae is the same as that of *Sarcandra* spp (Crété 1957). Crété stated that the embryonic development of *Houttuynia cordata* resembles that of the Polygonaceae and the Nyctangiacea. The Chloranthales and the Piperales seem to have closer affinity to the Polygonales and the Caryophyllales than the Magnoliales, in which the embryonic development is the Geraniad type or its variation.

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山崎　敬：センリョウ（センリョウ科）の胚発生とセンリョウ科の系統学上の位置

センリョウ科はドクダミ科と共に双子葉植物の原始的な群として扱われたり，モクレン目群からの特殊化した群として扱われたりしている．最近は主に後者の見解が支持されている．胚形成は科や目によってほぼ一定していて，系統関係の研究には重要な手掛かりとなる．今回の観察によりセンリョウの胚形成はPolygonad typeで，ドクダミ科のドクダミと同じであることが明らかとなった．このことからするとセンリョウ科やドクダミ科はタデ目やナデシコ目と関係があるものと考えられる．近縁とされるLactoridaceaeやTrimeniaceaeでは胚形成の詳細な研究はされていないが，花の構造はセンリョウ科とは基本的に異なるから，モクレン目との関連は考えられない．DNAからの結果とは，センリョウ目が原始的であることは一致するが，他の目や科との類縁関係は一致しない．この点については今後の研究が必要である．

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